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Phenotypic and genetic parameters for selected production and reproduction traits of Mpwapwa cattle in low-input production systems

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Abstract

The objective of this study was to assess the genetic improvement programme of the Mpwapwa dairy cattle breed over the past four decades, based on on-station selection and breeding. Estimates of genetic parameters and genetic trends for total lactation milk yield (LMY), 305-day lactation milk yield (305LMY), lactation length (LL), age at first calving (AFC), and calving interval (CI) were derived. The study used 1,003 lactation records from 385 cows and 78 sires collected from 1967 to 2012. Genetic parameters were estimated using an animal model procedure with ASReml software. The heritability for LMY and 305LMY were moderately high (0.33 ± 0.11 – 0.44 ± 0.04) and low for LL (0.13 ± 0.17). Repeatability for LMY and 305LMY was high (0.62 ± 0.04 – 0.70 ± 0.03) and moderate for LL (0.27 ± 0.06). The heritability for AFC (0.13 ± 0.11) and CI (0.10 ± 0.05) were low. The repeatability for CI was low (0.10 ± 0.05). Genetic correlation of 305LMY with LMY and CI were 0.87 ± 0.02 and -0.06 ± 0.009 , respectively, while the corresponding phenotypic correlation estimates were 0.82 ± 0.01 and -0.01 ± 0.001 . Variation among animal estimated breeding values (EBV) was significant, suggesting that selection to improve these traits is feasible. Thirty seven out of 78 sires had favourable EBV (0–900 kg) for milk yield, which suggests that selection for specific sires could result in increased LMY. Annual rates of sires EBV change for 305LMY, LL, CI, and AFC were -0.05, 0.15, and -0.14 days, respectively. All these traits showed that a decline in genetic progress for Mpwapwa dairy cattle in the on-station breeding programme.

Keywords: Fertility, genetic correlation, genetic trend, milk yield, variance components

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Introduction

The realized productivity of indigenous breeds in the tropics is generally low, with estimates of lactation milk yield ranging from 300 to 1,100 kg (Rege *et al.*, 2001; Tadesse & Dessie, 2003). Crossbreeding of tropical indigenous breeds with temperate dairy breeds has been used in various countries as a means of increasing milk production and as a major strategy that has contributed to improving and expanding the dairy cattle population and milk production in the tropics (Cunningham & Syrstad, 1987). Dual-purpose breeds with mixed zebu (*Bos indicus*) and temperate breeds (*Bos taurus*) have shown increased productivity in low-input production systems (Peixoto *et al.*, 2006; Madalena *et al.*, 2012). Most of the countries in sub-Saharan Africa have chosen Holstein-Friesian, Ayrshire, Jersey, and their corresponding crosses with *Bos indicus* for dairy production. With dairy intensification increasing, farmers have adopted high-producing grade exotic *Bos taurus* breeds (Chagunda *et al.*, 2015). However, farmers in low-potential areas have opted to use genotypes with unique genetic characteristics, such as adaptation to heat and drought, tolerance to disease, and efficient utilization of low-quality forages (Gebreyohannes *et al.*, 2013).

In Tanzania, the Mpwapwa breed, a composite dual-purpose breed suitable for milk and meat production in medium - to low-input production environments, was created by crossing East African Zebu, Indian Zebu, and European dairy breeds, mainly Ayrshire. Establishing the Mpwapwa breed started in the 1920s and ended in 1958 (Kiwuwa & Kyomo, 1970; Rushalaza & Kasonta, 1993). Since then, the breed has been kept for both milk and meat production. According to Kiwuwa & Kyomo (1970), the genetic constitution of Mpwapwa cattle consists of 32% Red Sindhi, 30% Sahiwal, 19% Tanganyika Shorthorn Zebu (TSZ), 11% Boran, and 8% *Bos taurus*, mainly Ayrshire. The breeding goal was for cows to produce 2,300 kg of milk

yield per 305-day lactation and for steers to reach a carcass of 230 kg in less than four years in low-input dairy production systems (Syrstad, 1990; Bwire *et al.*, 2005). A nucleus was established in 1958 to drive the breeding programme (Syrstad, 1990).

The major challenge has been how to scale up a breeding programme to cover the needs of a wider breeder and consumer community. The breed multiplication plan has not been efficient, owing to a high turnover of animal breeding experts, disease outbreaks, and policy changes (Wilson, 2009). The challenge has been how to multiply a large number of animals and distribute them to farmers. For example, in the 1990s, the Mpwapwa cattle population was reduced because of mortalities caused by East Coast Fever (ECF), which led to the near extinction of the breed (Bwire *et al.*, 2005). The low Mpwapwa cattle population (<1,000 females) had led the Food Agriculture Organization of the United Nations (FAO, Rome) to characterise Mpwapwa cattle breed as being at risk of extinction (Syrstad, 1990; Rege, 1999). However, multiplication efforts from 1999 onwards have increased the population of the breed owing to farmers' increased demand for the improved cows and bulls. The efforts have involved multiplication of the pure Mpwapwa breed and intensification of the increase in number of the animals by backcrossing the present pure Mpwapwa with Boran and Sahiwal. The assumption was that Mpwapwa breed production potential is on par with Sahiwal, while Boran cows were chosen because they are known to be better milkers than TSZ (Bwire *et al.*, 2005).

The target of 2,300 kg of milk per 305-day lactation has not been realized, while the goal of 230 kg carcass per steer at the age of less than four was realized in 1985. There have been efforts to introduce Mpwapwa cattle on-farm since the 1970s under an open nucleus breeding schemes. The breed performance on-farm showed that Mpwapwa cows were yielding four times more milk and had higher growth rates than TSZ cows (Rushalaza & Kasonta, 1993). The breed has been widely accepted by the community owing to its adequate milk and meat yield, disease resistance, and the ability of the bulls to be used for draught power (Komwihangilo *et al.*, 2009).

The selection of the best cows and bulls was based on phenotypic records for diseases, lactation performance, fertility, growth rate, and temperament. Genetic parameters and evaluations of these traits have not been calculated before. However, to develop a sustainable breeding programme, it is important to estimate the variance components and genetic parameters, such as heritability and repeatability for production and fertility traits. Variance components and genetic parameters are key factors for prediction of selection response for a particular breeding programme. The availability of estimated breeding values (EBV) for production and fertility traits in Mpwapwa cattle population will help develop optimal selection and mating strategies of superior cows and bulls in an optimal breeding programme.

The objective of this study was therefore to estimate genetic parameters and breeding values of individual animals, and determine the genetic progress that has been achieved over the past four decades in Mpwapwa breed through nucleus breeding programme.

Materials and Methods

Data for the present study were acquired from the Tanzania Livestock Research Institute, Mpwapwa, Tanzania. The research institute farm is located at 1,100 m above sea level in the semi-arid zone of central Tanzania. The average annual rainfall at the institute is 660 mm, of which more than 90% falls between December and April. The mean daily temperature is 26 °C, with the minimum temperature of 13.8 °C in August and a maximum of 30.2 °C in November. The production seasons are divided into the wet (December to June) and dry season (July to November). The farm is dominated by natural pastures consisting mainly of *Hyparrhenia* spps, *Brachiaria brizantha*, *Cynodon dactylon*, *Chloris gayana*, *Cenchrus ciliaris*, *Heteropogon contortus*, and *Panicum maximum*. These are considered suitable forage grasses. However, their distribution and quantity vary between the two seasons of the year (Katyega, 1987; Greenway, 1933; Bwire & Wiktorsson, 2003). Before 1998, the average herd size was greater than 1,000 animals (Syrstad, 1990). However, since 1999, the herd size has remained below 1,000 animals (Bwire *et al.*, 2005; ILRI, 2009). All cows were grazed on natural pastures from 7:30 am to 3:00 pm and received a certain amount of concentrates, composed of maize bran, minerals and sunflower or cotton seed cake during milking. Livestock management included control of parasites and diseases through dipping, deworming, and vaccination. Cows with less than 1,000 kg lactation milk and 84 days in LL were culled from the herd. Cows with milk yield above 2,000 kg were considered elite. The restricted suckling method was applied in which three teats were milked and one was left for the calf to suckle until weaning at the age 90 days. After weaning, all teats were milked with a deliberate drying off at 305 days for cows with longer LL (Bwire *et al.*, 2005).

A total of 3,700 total lactation milk yield records for cows calving from 1967 to 2012 were retrieved. Data for milk yield were recorded daily. The individual cow record card consisted of birth date, calving date, parity, LMY, and LL. Reproduction traits, such as AFC and calving interval (CI), were calculated using birth

dates and calving dates, respectively. Production traits included total LMY, 305-day LMY (305LMY), and LL. Total lactation yield was adjusted to 305 days to account for cows that had been sold or had died before completing the lactation. The dataset consisted of the Mpwapwa crossline (F1) of 56% *Bos taurus*, first backcross (R1) of 34% *Bos taurus*, inter-se of 34% *Bos taurus*, Mpwapwa crosses with Boran and Sahiwal, and pure Mpwapwa with 8% *Bos taurus*. Only data for cows with breed composition of 8% *Bos taurus* that were regarded as pure Mpwapwa breed were retained for analysis. Cows with a LL of less than 100 days were excluded in the analysis. Each cow used for data analysis had at least one parent of known pedigree information. After data editing, 1,003 lactation records from 385 Mpwapwa cows were retained for analysis.

Statistical Analysis System (SAS, 2011, version 9.3) software was used in sorting, summarizing, merging, creating new variables, and combining datasets. The restricted maximum likelihood (REML) procedure was used to estimate (co)variance components for production and reproduction traits with the ASReml version 3 software program (Gilmour *et al.*, 2009). The following repeatability animal model was fitted for milk yield, LL, and CI. For AFC no permanent environmental effect was fitted as there was always only a single record per animal:

$$y = X\beta + Za + Wpe + e$$

Where: y is a vector of phenotypic observation of traits

β is vector of fixed effects

a is a vector of additive genetic random effects

pe is a vector of permanent environment of cow random effects

e is the vector of random error effects

X, Z, W are the respective incidence matrices

Fixed effects included year-season of calving, parity number (except for AFC), and LL (for LMY only).

It was assumed that the expectation (E) of y (Ey) = $X\beta$; $E(a) = 0$ and $E(e) = 0$. the $\text{var}(a) = A\sigma_a^2 = G$, $\text{var}(pe) = I\sigma_{pe}^2$ and $\text{var}(e) = I\sigma_e^2 = R$; hence, $\text{var}(y) = ZAZ'\sigma_a^2 + W I \sigma_{pe}^2 W' + R$, with A being the numerator relationship matrix between the animals of the study and A^{-1} is the inverse of A (Henderson, 1973; Mrode & Thompson, 2005). Heritability (h^2) was calculated as:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2)$$

and repeatability (r) was calculated as

$$r = (\sigma_a^2 + \sigma_{pe}^2) / (\sigma_a^2 + \sigma_{pe}^2 + \sigma_e^2).$$

Solutions of the animal effect constituted individual animal EBVs. Phenotypic trend was obtained by plotting a mean of performance of a trait by year of calving, while the genetic trends were derived with the mean yearly EBVs.

A series of bivariate analyses based on the above model were also conducted to estimate phenotypic and genetic correlations among the traits.

Results and Discussion

A summary of descriptive statistics for production and reproduction traits evaluated in this study are presented in Table 1. There was large variation among cows for LMY (34%) and CI (26%). The current lactation yield was lower than that reported by Mchau and Syrstad (1991) (1,519–1,560 kg) and Rushalaza & Kasonta (1993), but similar to the previous on-station estimate of 1,446.4 kg (Das *et al.*, 1999). Owing to the lack of on-farm performance records for the Mpwapwa breed, it was difficult to compare current on-station lactation yield with on-farm performance. The differences observed in LMY of Mpwapwa from various studies may be due to variations in environment conditions and levels of management of the animals in different years. The mean milk yield observed in the present study was within the range of 1,000 to 2,477 kg of lactation milk yield reported for improved zebu in the tropics (Cunningham & Syrstad, 1987) and crossbred dairy cows for smallholder dairy farmers under intensive production systems in Tanzania (Msanga *et al.*, 2000; Chenyambuga & Mseleko, 2009).

The overall mean LL for all lactations was 271.4 ± 44.7 days. The number of days in milk was generally moderate compared to the standard 305 days. The LL for the current study was higher than for previous on-station studies (228 days) (Das *et al.*, 1999) and lower than for on-farm studies (300 days) (Rushalaza & Kasonta, 1993). However, the LL observed in the present study was lower than the 278.7 to 326 days reported for crossbred cows in smallholder dairy farms in sub-Saharan Africa (Banda, 1996; Chenyambuga & Mseleko, 2009; Gebreyohannes *et al.*, 2013). A number of studies in sub-Saharan Africa have shown that an increase in number of days in milk is associated with an increase in LMY (Ngongoni *et al.*, 2006; Chenyambuga & Mseleko, 2009). Therefore, the low mean LL in the current study can be associated with low LMY of the Mpwapwa breed compared with other crossbred dairy cows.

Table 1 Means and standard deviations for production and reproduction traits of Mpwapwa cows from 1967-2012

Parameters	N	Mean ± SD	95% Confidence Interval		Min	Max	CV (%)
			Lower	Upper			
Milk production parameters							
LMY (kg)	1,003	1,480.0 ± 506.3	1,448.7	1,511.3	805.0	3,481.0	34.2
305LMY (kg)	1,013	1,686.0 ± 578.6	1,650.2	1,721.8	810.5	4,770.43	34.2
LL (days	1,013	271.4 ± 44.7	269.1	274.2	102.0	305.0	16.5
Reproduction parameters							
CI (days)	467	493.1 ± 130.7	481.3	505.0	351.0	899	26.5
AFC (months)	527	32.0 ± 7.1	31.4	32.6	28.0	62.0	22.2

Min: minimum, Max: maximum, CV: coefficient of variation, LMY: total lactation milk yield, 305LMY: 305-day lactation milk yield, LL: lactation length, CI: calving interval, AFC: age at first calving

The long mean CI of 493.1 days observed in this study is comparable with 402 to 480.4 days reported by previous studies in Tanzania (Asimwe & Kifaro, 2007; Swai *et al.*, 2007; Chenyambuga & Mseleko, 2009). The current study indicated that CI (493.1 \pm 130.7) was almost twice that of LL (271.4 \pm 44.7 days), implying that there was a long period when cows were not lactating or pregnant and, therefore, not productive. Bozworth *et al.* (1971) associated longer CI with inefficiency in heat detection, conception rate, and reproductive health in larger farms.

About 95% of the heifers calved at an age between 31.4 and 32.6 months. The AFC of the present study was within the range of 31.3 to 36.6 months of AFC for tropical crossbred heifers (Asimwe & Kifaro 2007; Yifat *et al.*, 2009) and dual-purpose synthetic breeds (Galukande *et al.*, 2013). Improvement in the production environment may enhance the growth rate and maturity of the heifers, and hence reduce AFC. Reduced AFC has been associated with increased productivity per herd life and reduced cost of rearing heifers (Teke & Murat 2013). The differences in milk production and LL for cows calving in the wet and dry seasons were not statistically significant. The non-significant effect of the season on the production variables may be attributed to management, mainly feeding management of milking cows, which allows them to maintain physiological balance and react positively to seasonal variations. However, the year of calving significantly affected production traits. The effect of year of calving may be associated with changes in management systems and climatic factors over the years.

The mean yearly LMY, 305LMY and LL showed a general declining trend (Figure 1) with some periodical increase and decrease throughout the study period. Cows calving between 1973 and 1984 had better performance than cows that calved between 1985 and 2000. The increase in milk yield from 1973 to 1984 could be explained by active breeding activities (Syrstad, 1990; Bwire *et al.*, 2005). It was during this period that the breeding target for beef production was realized. However, the target of 2,300 kg milk per lactation of 305 days was not reached. The declining milk production trend between 1985 and 1993 could be due to limited funding for research and production services because of the structural adjustment policy of the International Monetary Fund and World Bank to ensure debt repayment and economic restructuring of developing nations. As a result, most countries in Africa, including Tanzania, reduced their spending on health, education, and development activities, including research. During this period, most of the parastatal farms were reduced in size or privatized (Heidhues & Obare, 2011). This led to a decline in the number of breeding cows, followed by reduced selection pressure for best cows and bulls. The failure of public expenditure cut policies led the government and other donors to revive previous efforts to expand parastatal sectors. As result, the upward trend from 1994 could be explained by active support of the government on breed multiplication through projects such as Tanzania Agricultural Research Project Phase II (TARPII) (Nankani *et al.*, 2004) and Agricultural Sector Development Programme (URT, 2006). However, it is apparent from this study that the level of milk production overall has not increased for the past 40 years. The current management strategy needs to be revised to attain the desired breeding goal of the 2,300 kg of milk per lactation. The Mpwapwa breed, like any other crossbred dairy animals in the tropics, is vulnerable to disease and lack of feed resources. Additional management of the animals in terms of general husbandry and feeding strategies is required. In addition, the current genetic improvement programme needs to adopt new

technologies of feeding, reproduction and genotyping to improve the environment, fertility and selection of cows and bulls with an acceptable range of breed composition.

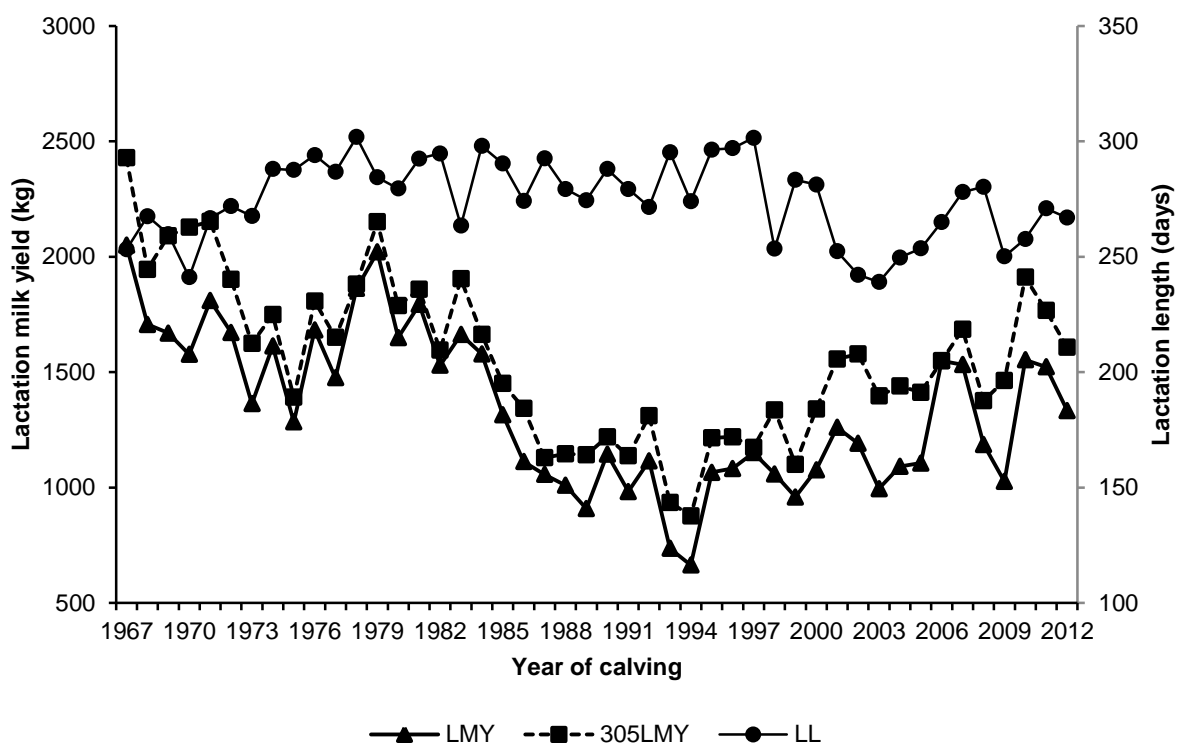


Figure 1 Phenotypic trend of yearly mean lactation milk yield, 305-day lactation milk yield and lactation length for Mpwapwa breed
LMY: lactation milk yield; 305LMY: 305-day lactation milk yield; LL: lactation length.

Figure 2 shows an increase in AFC from 1967 to 2012, while the CI interval remained almost constant. Increase in AFC over time in the present study could be attributed to management factors, leading to a poor conception rate of heifers that tend to remain in herd for a long time. The breeding protocol for Mpwapwa requires heifers that weigh less than 200 kg at the age of two to be culled. However, this has not been practised owing to the small number of females that were available for breeding (Bwire *et al.*, 2005). As a result, heifers that did not meet the mating criterion were retained for the next breeding season. The CI has remained between 400 to 500 days which is similar to other dairy cows in sub-Saharan Africa reported in previous studies (Chagunda *et al.*, 2004; Tadese *et al.*, 2010).

The genetic parameter estimates for production and fertility traits are presented in Table 2. With the exception of LL and AFC heritability, estimates were statistically greater than zero ($P < 0.05$). Heritability estimates for 305LMY was higher than for LMY. Heritability estimates for milk production traits were within the range of previous estimates for improved zebu and crossbred cows in sub-Saharan Africa (Mwatawala *et al.*, 2002; Demeke *et al.*, 2004; Ilatsia *et al.*, 2007). Heritability estimates for LMY and 305LMY were moderately high, which implies that the trait could be used for the genetic improvement of the breed via selection. The heritability estimate of 0.13 ± 0.11 for AFC was higher than for Sahiwal cattle and crossbred cows (Mwatawala *et al.*, 2002; Amimo *et al.*, 2006; Ilatsia *et al.*, 2007), but lower than for purebred Holstein-Friesians in Malawi (0.2) (Chagunda *et al.*, 2004) and Kenya (0.38) (Ojango & Pollott, 2001). Heritability value for CI was low (0.10), which is similar to improved zebu and crossbreds (Mwatawala *et al.*, 2002; Ilatsia *et al.*, 2007), but lower than Kenyan Holstein Friesians (Ojango & Pollott, 2001).

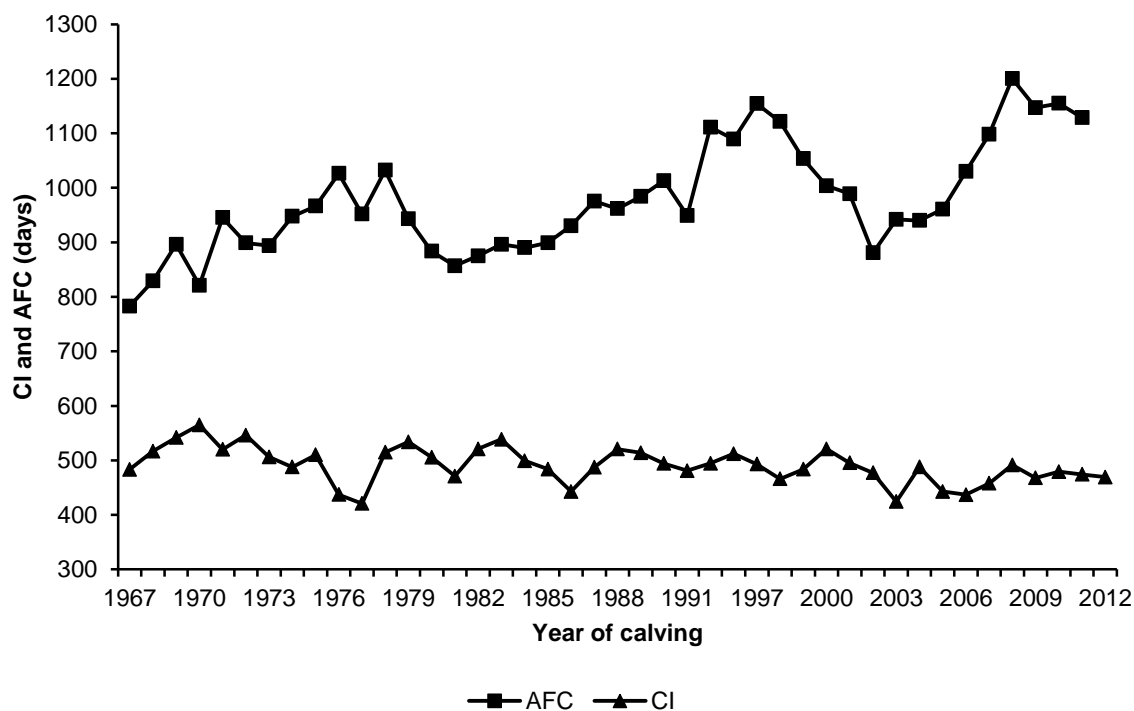


Figure 2 Phenotypic trend of yearly mean age at first calving and calving interval for Mpwapwa breed
AFC: age at first calving; CI: calving interval.

Heritability for AFC and CI is generally considered low, which suggests that these traits are affected by environment and other farm management policies more than additive gene action. The higher standard error for heritability estimates for AFC could be due to the small number of records, data structure, and historical background of the development of the breed. Therefore, more records may be required for further evaluation of the traits. However, it is possible to reduce CI and AFC by improving feeding and fertility management of the animals. Improved feeding management and culling of heifers with low body weight at the age of 72 weeks could reduce the age at first mating because of improved growth and early maturity. On the other hand, heifers and cows that are well fed are likely to undergo normal cyclic behaviour and therefore to improve both AFC and CI. Studies in temperate countries have suggested the possibility of selection for reduced CI by using other genetically correlated traits such as body condition score and milk progesterone (Dal Zotto *et al.*, 2007; Nyman *et al.*, 2014). A decrease in AFC and CI would reduce the cost for herd replacement and maximize the longevity and the productive life of a cow. Therefore, in the current breeding scheme, genetic gain for reproductive traits could be improved by culling poor performing animals and improving environment and management strategies.

Repeatability estimates for production traits ranged from moderate for LL (0.27) to high for LMY and 305LMY (0.62-0.70). The estimates for LMY and 305LMY were higher compared with previous studies of improved zebu in low-input production systems in sub-Saharan Africa (Ilatsia *et al.*, 2007; Badri *et al.*, 2011). Conversely, the repeatability estimates for LL was moderate, but consistent with other studies of improved zebu in the tropics (Ilatsia *et al.*, 2007; Badri *et al.*, 2011; Santos *et al.*, 2013). The repeatability estimates for production traits indicate that selection of the best cows to be kept in the herd for production could be done with some degree of precision based on estimates for LMY, 305LMY and LL of the cows.

The repeatability for CI (0.10) was low, which is consistent with other previous studies for crossbred cows in sub-Saharan Africa (Chagunda *et al.*, 2004; Ilatsia *et al.*, 2007). The low genetic parameter estimates could be owing to the small number of records for CI used in this study. Furthermore, the repeatability value was the same as heritability because of no permanent environment variance, suggesting that researchers may not predict the future CI of the same cow from her current records any better than predict the CI of her progeny.

Table 2 Estimates of additive genetic variance (σ^2_a), variance due to permanent (σ^2_{pe}), phenotypic variance (σ^2_p), residual variance (σ^2_e), heritability ($h^2 \pm SE$) and repeatability ($r \pm SE$) for production and reproduction traits for Mpwapwa cows

Parameter	LMY (kg)	305LMY (kg)	LL (days)	CI (days)	AFC (Month)
σ^2_a	78,920.0	169,100.0	242.99.0	1,6524.0	2,248.20
σ^2_p	242,790.0	382,190.0	1,854.5.0	1,6877.0	17,549.0
σ^2_{pe}	73,070.97	95,595.30	261.67.0	0.00005.0	—
σ^2_e	90,795.30	117,486.0	1,349.81.0	15,224.20	15,300.60
h^2	0.33 \pm 0.11	0.44 \pm 0.04	0.13 \pm 0.17.0	0.10 \pm 0.05	0.13 \pm 0.11
r	0.62 \pm 0.04	0.70 \pm 0.03	0.27 \pm 0.06	0.10 \pm 0.05	—

Phenotypic and genetic correlations for production and reproduction traits are presented in Table 3.

Table 3 Phenotypic (below the diagonal) and genetic (above the diagonal) among production and reproduction traits

Trait	305LMY	LMY	CI	AFC
305LMY		0.87 \pm 0.02*	-0.06 \pm 0.009*	0.0
LMY	0.82 \pm 0.01*		0.15 \pm 0.11	0.0
CI	-0.01 \pm 0.001*	0.06 \pm 0.05		0.0
AFC	-0.11 \pm 0.0	-0.12 \pm 0.0	-0.10 \pm 0.0	

*Correlations between parameters are significantly different from zero

The phenotypic (0.82) and genetic (0.87) correlations between 305LMY and LMY were high, positive, and significantly different from zero. Phenotypic and genetic correlations between 305LMY and CI traits were low and closer to zero, but significant from zero (-0.01 and -0.06). The low phenotypic correlation between 305LMY and CI traits is consistent with other studies in the tropics for purebred and crossbred dairy cows (Syrstad, 1993; Adeoye & Ogundipe, 2011). However, Ilatsia *et al.* (2007) and Rehman *et al.* (2008) reported higher and positive phenotypic correlation between lactation milk yield and CI for Sahiwal cows in the tropics. The genetic correlation between production and reproduction traits from the current study was within the range of -0.64 –0.91 reported for improved zebu and crossbred dairy cows in the tropics (Ojango & Pollott, 2001; Rehman *et al.*, 2008; Zeleke *et al.*, 2016). A low genetic correlation between 305LMY and CI indicates a weak genetic and physiological relationship between the traits. A low genetic relationship indicates a necessity for improvement of reproductive management and further investigation of environmental factors controlling the traits. Phenotypic and genetic correlations between production and reproduction traits were low, suggesting that selection for one trait group will not affect the other. Therefore, there is not sufficient evidence that selection based on reproductive traits would lead to increased milk yield. However, selection based on 305LMY may lead to higher response in milk production.

The calculated rate of inbreeding depression was 0.24% per generation based on the data used. This might not be a true representative value of the population because of the small pedigree information used in this particular study. The true picture would have been attained if all animals involved in a breeding programme had been recorded. However, the current study showed lower inbreeding depression. This could be because of factors such as pedigree size and mating strategies applied at the farm. Therefore, there is no evidence to conclude that the declining trend in production and fertility traits is associated with inbreeding depression.

Average EBV for 305LMY of individual animals by year of birth are presented in Figures 3a & 3b for sires and cows, respectively. The genetic trend for both sire and cow EBV for milk production was negative, which indicates a reduction in the genetic propensity of the animals to produce milk over time. The overall rates of EBV change were -3.0kg/year for sires and -1.2kg/year for cows. Various factors might have led to these trends, including intensive selection of cows and bulls for high milk yield between 1968s and 1985.

The declining trend of genetic progress in 1985, followed by an increase in 1994, can be explained by changing policies. The adoption of public expenditure cuts in 1980s affected both production and social services such as research and extension (Heidhues & Obare, 2011). However, the positive genetic trend since 1994 may be explained by government strengthening research institutions and extension services (URT, 2006). The overall negative genetic progress may be linked to longer generation intervals as a result of delayed age at first calving and longer CIs. Similar trends in EBV for milk yield have been observed in multi-breed populations of dairy cattle in Ethiopia (Gebreyohannes *et al.*, 2013). Studies on Brazilian improved zebu such as Gry and Guzerat (Verneque *et al.*, 1996, Peixoto *et al.*, 2006) have shown that positive genetic progress for milk yield can be achieved in a tropical environment when appropriate selection

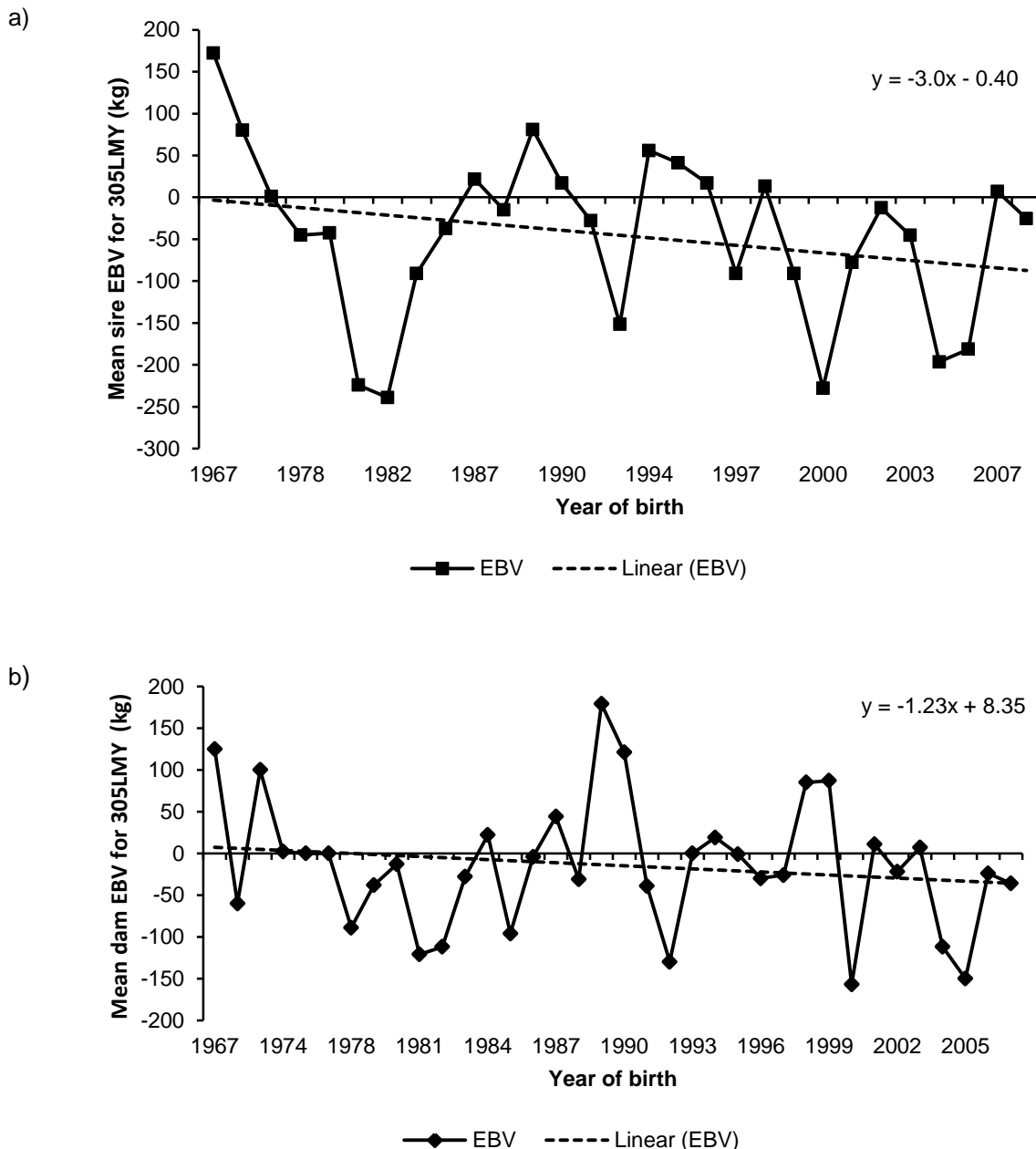


Figure 3 Trend in estimated breeding values for 305 days' lactation milk yield by year of birth for a) sire and b) cow
EBV: estimated breeding values; 305LMY: 305-day lactation milk yield.

strategies are in place. For example, Peixoto *et al.* (2006) reported an annual genetic gain of 7.0 kg per year for the Guzarat breed in Brazil. Selection and culling processes practised to date have been suboptimal because parents were selected based on their phenotypic performance rather than EBV.

The genetic trend for LL was negative, which indicates a decrease of -0.05 days per year (Figure 4). The decrease in LL attributed to a reduced 305LMY. Studies in the tropics have reported a positive phenotypic and genetic correlation for LMY and LL for improved zebu (Dahlin *et al.*, 1998), which indicates that selection for milk yield, accompanied by improved management, could improve LL. In the tropics, LL is used as a measure of persistency in milk production as result of climatic challenges, which is contrary to temperate dairy breeds where LL is used as a measure of milk yield, and a decrease in milk production is caused mainly by the advanced stage of gestation (Syrstad, 1990).

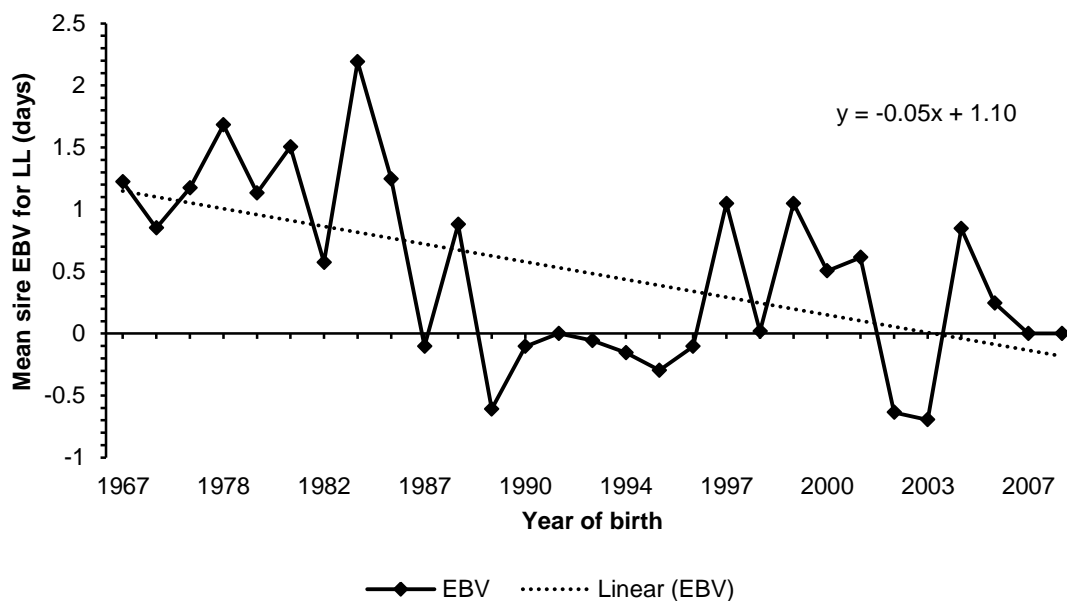


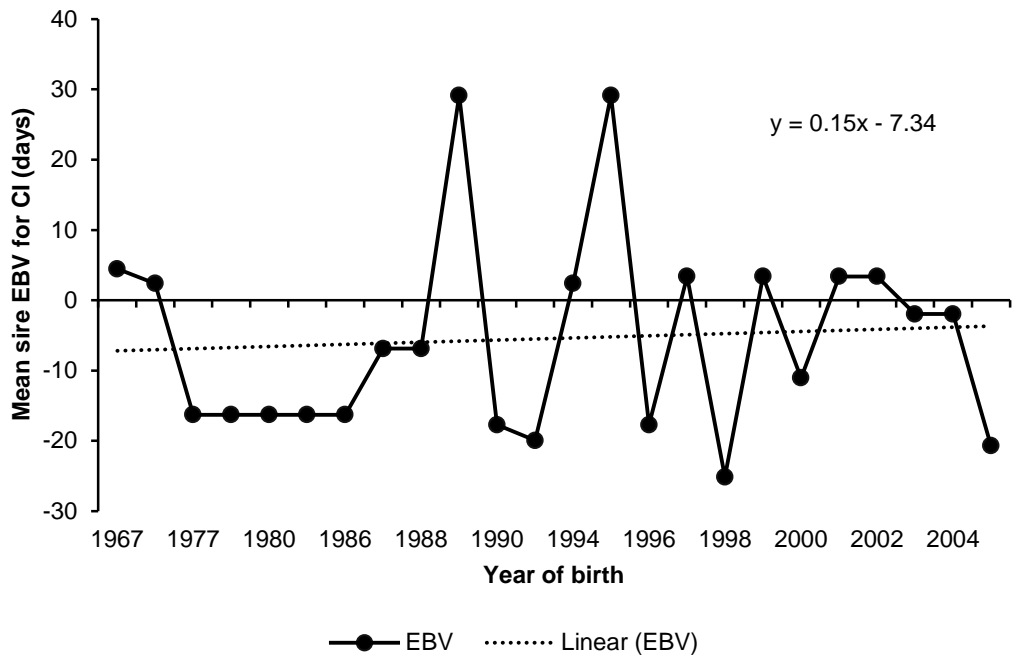
Figure 4 Genetic trend of sire estimated breeding values for lactation length (days) of the Mpwapwa breed EBV: estimated breeding values; LL: lactation length.

The genetic trends of sires for CI and AFC have remained close to zero (Figure 5a & 5b) over time. Since the Mpwapwa breeding scheme emphasizes milk and meat yield, reproductive traits could be improved by selecting heifers with higher growth rates and by closer monitoring and culling of cows with poor fertility. These two traits have low heritability. Therefore, environmental effects such as feed, care, and disease resistance play a significant role in their improvement.

The distribution of sire EBV for 305LMY ranged from -600 to +900 kg of milk per lactation (Figure 6), while for LL it ranged from -8.3 to 15.6 days. On the one hand, 37 out of 78 sires had favourable (0–900kg) EBV for milk yield, suggesting the possibility of selecting sires, leading to positive genetic gain. On the other hand, 53 bulls had EBV for LL ranging from 0 to +10 days, indicating a wide choice of bulls for favourable increase in LL, if this ever becomes part of the breeding goal.

Estimated individual sire breeding values for AFC and CI varied from -50 to +150 days and -45 to +50 days, respectively. The observed variation in EBV between animals in the present study supports the feasibility of selecting cows and bulls as parents in a breeding programme over multiple years. Although the two traits were found to be low in heritability, individual bulls with negative EBV for CI and AFC may be selected as potential sires in the breeding programme. Improvement of fertility traits is necessary for a successful dairy enterprise, since regular calving at a minimal interval is essential for constant milk production all year round. Long CIs owing to genetic and non-genetic factors would lead to low productivity and slow genetic progress over time.

a)



b)

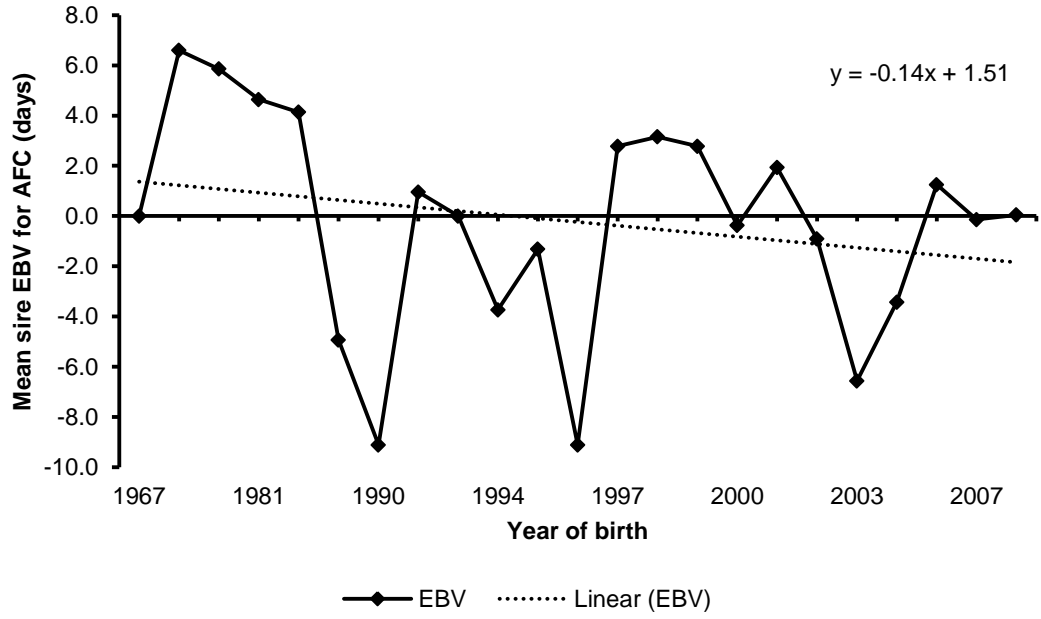


Figure 5 Trend in for a) calving interval and b) age at first calving in days of Mpwapwa cows
EBV: estimated breeding values; CI: calving interval; AFC: age at first calving

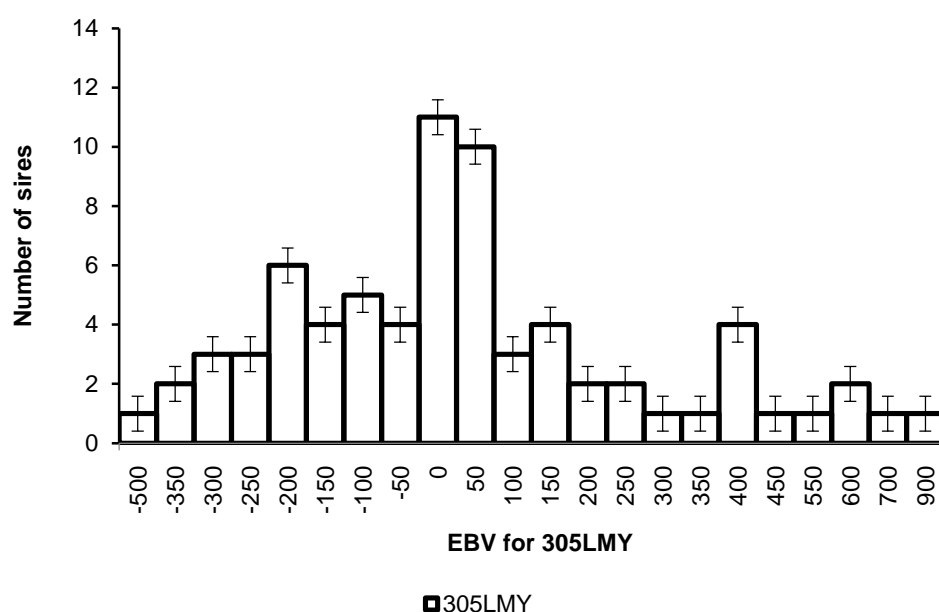


Figure 6 Distribution of sire estimated breeding values for 305-day lactation milk yield of Mpwapwa breed with error bars representing standard errors of means
EBV: estimated breeding values; 305LMY: 305-day lactation milk yield.

Conclusion

Phenotypic and genetic correlations between 305LMY and LMY were high, positive, and significantly different from zero. This suggests that 305LMY could be used an important selection criterion for increased milk yield. The genetic correlation between 305LMY and CI was low, suggesting that selection for one trait would not affect the other. All these traits of the Mpwapwa breed have shown an overall decline in phenotypic and genetic progress over the past four decades. This could be owing to unsystematic breeding policies and weak monitoring of the genetic progress. Thus, systematic planning of the genetic improvement programme of the breeding scheme is essential to avoid a declining genetic trend for production and reproduction traits. A favourable trend could be established in this programme and transferred to smallholder dairy production systems. Further understanding of the performance of the breed in a smallholder dairy production system is required for an effective and sustainable genetic improvement programme.

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Authors' Contributions

ARC conducted the research during his PhD studies and was responsible for drafting, analysing data and submitting the manuscript. MGGC, GB, AP and DMK coordinated the study, critically analysed and interpreted the results and participated in the manuscript development.

Conflict of Interest Declaration

The authors of this paper declare that there is no conflict of interest. They confirm that the order of listing authors has been agreed by them and the manuscript has been read and approved by all authors.

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